ANNALS OF CARNEGIE MUSEUM

Vol. 63, Number 2, Pp. 105–113 31 May 1994

PALAEOPHICHTHYS PARVULUS EASTMAN, 1908, A GNATHORHIZID DIPNOAN FROM THE MIDDLE PENNSYLVANIAN OF ILLINOIS, USA

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Abstract

Palaeophichthys Eastman, 1908 is a gnathorhizid dipnoan. *Monongahela* Lund, 1970, a taxon based on isolated tooth plates, is its junior synonym. *Palaeophichthys* has tooth plates and a shoulder girdle typical of a gnathorhizid. The genus is distinct from *Gnathorhiza* in the skull-roof pattern (unpaired median B-, C-, E- and F-bones) and in details of the tooth plates (the fourth tooth ridge originates lateral to the apex). The genus *Palaeophichthys* ranges from Middle Pennsylvanian to Early Permian in east-central North America.

Introduction

In an unlikely place—a volume on the Devonian fishes of Iowa—Eastman (1908) erected the monotypic genus *Palaeophichthys* (*P. parvulus*) based on a single specimen from the Middle Pennsylvanian of the Mazon Creek area, Grundy County, Illinois. His holotype, a tiny fish on counterpart halves of a typical nodule from Mazon Creek, had been part of the S. S. Strong collection, Accession No. [222]3 of the Peabody Museum of Natural History. Donated by Yale University to the Museum of Comparative Zoology at Harvard College, it was catalogued as MCZ 5090a+b. Working from the unprepared specimen, on which much of the detail was obscured by an infilling of white kaolin, Eastman provided only a superficial description and a sketchy line drawing in which the eye and gaping mouth were wholly imaginary. The magnification of his figure was mis-stated as "×2-1" instead of the actual ×3 (Schevill, 1932). In default of morphological detail, Eastman attempted to classify his new genus, *Palaeophichthys,* mainly on the basis of a median fin, in which the dorsal is confluent with the caudal and anal. He mentioned a similar confluent unpaired fin in the dipnoans *Phaneropleuron* and *Uronemus,* but found other features that suggested affinities with coelacanths. "On the whole," he concluded, "the most plausible interpretation of *Palaeophichthys* seems to be to regard it as an aberrant and extremely degenerate offshot of fringe-finned ganoids adapted to a mud-grovelling mode of existence" (Eastman, 1908:254).

In a subsequent publication, Eastman (1917:272–273) added to the hypodigm of *Palaeophichthys parvulus* a second and topotypic specimen, USNM 4433 (*sic,* mis-cited as "4453") in the R. D. Lacoe collection at the National Museum of Natural History, Smithsonian Institution. From its water-worn condition this specimen, a half-nodule, appears to have been recovered from the bed of Mazon Creek itself. Aside from observations on the gross form and squamation of the fish, his second paper added no further information on its morphology or system-

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Submitted 23 November 1992.

atic position. "This peculiar crossopterygian genus," Eastman observed, "has been previously referred to the Coelacanthidae, but is distinguished from all other members of the family by its elongate, anguilliform body and continuous median fins. In the latter respect an agreement is to be noted with the specialized and problematical genus *Tarrasius,* from the Lower Carboniferous of Scotland, and also with *Conchopoma gadiforme* Kner, from the Lower Permian of Rhenish Prussia. Possibly both *Tarrasius* and *Conchopoma* should be regarded as aberrant coelacanths." The second specimen was illustrated by a retouched and slightly reduced photograph that reveals little morphological detail.

Lacking a proper description, later authors followed Eastman in assigning *Palaeophichthys* to either the Actinistia (coelacanths), to primitive actinopterygians (*Tarrasius*), or to the Dipnoi (*Conchopoma*). Jordan (1923) and Hay (1929) placed the Tarrasiidae with *Palaeophichthys* within the Actinistia; Zittel (1923, 1932) cited *Palaeophichthys* as probably within the Coelacanthidae. After Moy-Thomas (1934) demonstrated that *Tarrasius* is, in fact, a primitive actinopterygian, *Palaeophichthys* was regarded as an actinopterygian by Berg (1936), Romer (1945), Moy-Thomas and Miles (1971), and Bardack (1979). Jessen (1973) did not assign the genus to any group despite comparison with *Tarrasius* and other forms with a continuous fin fold, and Lehman had a similar approach (1966: "not a crossopterygian"). As the third group used for comparison by Eastman (1908, 1917), the dipnoans were suggested as the proper place for *Palaeophichthys* by Vorobyeva and Obruchev (1964: within Ctenodontidae together with *Ctenodus, Tranodis, Sagenodus, Megapleuron, Proceratodus,* and *Nielsenia*), Romer (1966: Dipnoi incertae sedis), Baird (personal communication in Bardack [1979:511]: "a senior synonym of the dipnoan *Conchopoma edesi* . . ."; and in Schultze and Bardack [1987:1]: ". . . a dipnoan, probably a new genus") and Carroll (1987:Dipnoi incertae sedis).

For most of the past half century, the type specimen has been inaccessible to researchers, having been borrowed around 1938 by T. Stanley Westoll of the University of Newcastle-upon-Tyne, England. Professor Westoll retired without publishing his conclusions on the affinities of *Palaeophichthys,* and in 1985 the specimen was returned. With the newly repatriated specimen in hand, the present restudy was undertaken to establish the true affinities of the fish.

The type and hypotype specimens have been prepared by removing the encrusting kaolin from the nodules with porcupine quills, insect pins, and small bristle brushes. Red latex casts (Baird, 1955) were then made from the natural molds.

SYSTEMATIC PALEONTOLOGY

Subclass Dipnoi Müller, 1845
Family Gnathorhizidae Miles, 1977
Genus *Palaeophichthys* Eastman, 1908
Synonym: *Monongahela* Lund, 1970
For synonymy list see Schultze (1992:200–201)

Diagnosis.—Gnathorhizid dipnoan with four unpaired median skull roof bones (B, C, E, and F). Pterygoid tooth plate with four ridges, the most posterior (fourth) ridge originating posterolaterally to the apex, whereas the other three diverge anterolaterally. Prearticular tooth plate with three ridges. Elongated body (depth = 9.5–12.5% of total length; head length = 14–15% of total length).

Range.—Early Westphalian D to Wolfcampian, Permo-Carboniferous.

Type species.—*P. parvulus* Eastman, 1908.

Palaeophichthys parvulus Eastman, 1908

Palaeophichthys parvulus, Eastman, 1908:253, fig. 37.
P. parvulus, Eastman, 1917:272, Pl. 10, fig. 2.
P. parvulus, Schevill, 1932:85.
P. parvulus, Vorobyeva and Obruchev, 1964:314.
P. parvulus, Jessen, 1973:177.
P. parvulus, Schultze, 1992:201.

Diagnosis.—Angle between first and second ridge of pterygoid tooth plate 40°, and between second and third ridge 28°.

Stratigraphic Position and Locality.—Francis Creek Shale, Carbondale Formation, Westphalian D, Middle Pennsylvanian; Mazon Creek area, Grundy County, Illinois, U.S.A.

Holotype.—MCZ 5090 a,b, complete specimen.

Holotype.—USNM 4433, poorly preserved complete specimen.

DESCRIPTION

A small, typical Mazon Creek concretion contains the holotype in part and counterpart; only one part of the concretion of the hypotype is preserved. As common for Mazon Creek, only the molds of the bones are preserved. The description is therefore based on latex casts prepared by Donald Baird, and the bones are described as if they are preserved three-dimensionally. The holotype is better preserved than the hypotype; thus the description refers mainly to the part and counterpart of the holotype.

The specimens are elongate but not eel-like as described by Eastman (1908). The holotype (Fig. 1) is 3.6 cm long with a depth of 0.45 cm, the hypotype is 5.2 and 0.7 cm, respectively. The head is 5.5 mm long (7.4 mm in hypotype), less than ⅙ of the total length. The part (MCZ 5090a) shows the right side of the specimen (MCZ 5090 a, Fig. 2), with the skull roof seen in oblique dorsal view; a smooth ostracod lies at the approximate place of the stomach. The counterpart (MCZ 5090 b, Fig. 3) shows bones of the left side and internal views of bones of the right side of the skull roof in oblique ventral view, and bones of the palate, gill arches, and shoulder girdle. Despite the small size, the skull roof, palate, and ceratohyal are fully ossified, and the complete body covered by scales.

Skull Roof (Fig. 2).—The skull roof displays three median bones, broad B- and C-bones, and a narrower E-bone. Only the inner side of the lateral portion of these bones can be seen in the hypotype. The posterior part of bone B, with its occipital commissure, is missing. The counterpart (Fig. 3) shows the impression of two small bones anterior to bone E, a median F-bone and the right lateral Q-bone with large evaginations for the pores of the supraorbital canal. The three median bones are displaced laterally over their neighboring bones toward the wide groove of the lateral line (Fig. 2). Only part of the inside of the left I and J bones, and part of the right J-bone in the corner between bones B and C are exposed. The anterior part of bone Z carries the broad lateral line canal, whereas the branching-off of the occipital commissure is only weakly preserved. In front of

Fig. 1.—*Palaeophichthys parvulus* Eastman, 1908. Latex cast of holotype MCZ 5090a dusted with NH_4Cl.

bone Z lies a small bone Y, followed anteriorly by a longer, only partly preserved X-bone. The pattern of the skull roof cannot be restored from the two specimens.

Cheek.—Because only a few bones are preserved behind the orbit, the cheek pattern cannot be established.

Lower jaw.—The right "angular" is completely preserved on the right side (Fig. 2), whereas only the posterior part of the left "angular" is preserved on the counterpart (Fig. 3). The position of the mandibular canal is marked as a deep

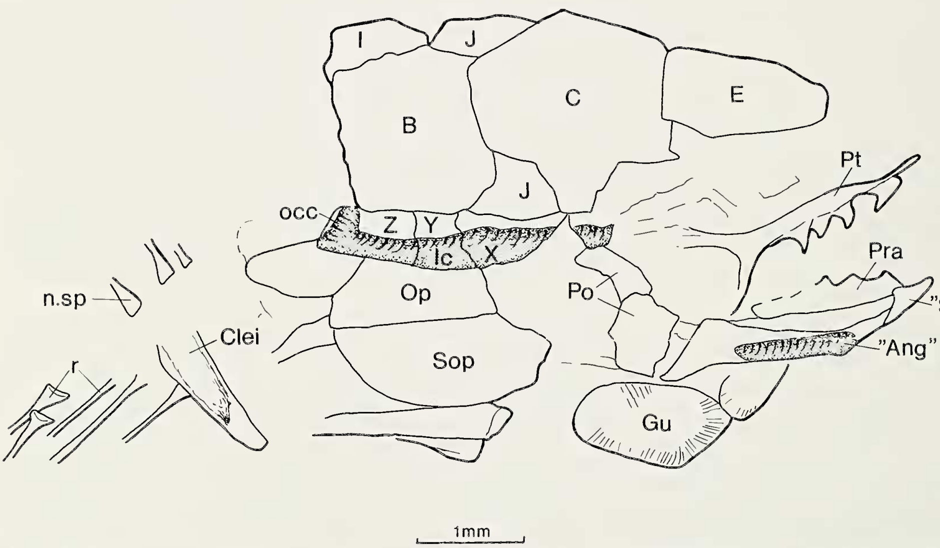

Fig. 2.—*Palaeophichthys parvulus* Eastman, 1908. Head of holotype MCZ 5090a. Abbreviations: "Ang," angular; B, C, E, I, J, X, Y, Z, skull-roof bones; Clei, cleithrum; Gu, gular; lc, main lateral canal; n.sp, neural spine; occ, occipital commissure; Op, operculum; Po, postorbital bone fragments; Pra, prearticular; Pt, pterygoid; r, rib; Sop, suboperculum, "Spl," splenial.

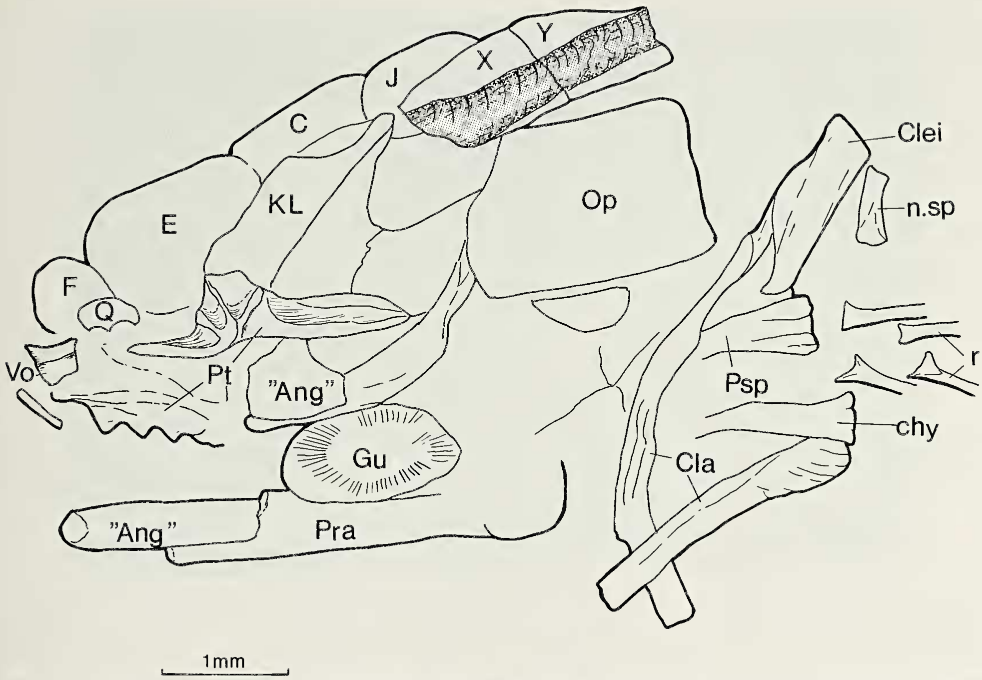

Fig. 3.—*Palaeophichthys parvulus* Eastman, 1908. Palate and shoulder girdle regions of holotype MCZ 5090b. Abbreviations: "Ang," angular; C, E, F, J, KL, Q, X, Y, skull roof bones from the inside; chy, ceratohyal; Cla, clavicle; Clei, cleithrum; Gu, gular; n.sp, neural spine; Op, operculum; Pra, prearticular; Pt, pterygoid; Psp, parasphenoid; Vo, vomer.

groove on the "angular." Anterior to the "angular" the "splenial" reaches anterolaterally to the prearticular. The labial side of the right prearticular is exposed partially on the part and the lingual side on the counterpart. The prearticular tooth plate is only seen in lateral view; it bears three ridges.

Palate.—Opposed to the tooth plate of the lower jaw, the tooth plate of the right pterygoid shows indication of four ridges. These ridges are clearly visible on the left pterygoid (Fig. 3, 4). A long anterior ridge is combined with three short ridges that are directed anterolaterally and posterolaterally. The first three ridges diverge from the apex of the tooth plate, whereas the most posterior ridge originates laterally to and lower than the apex. The ridges show indications of cusps. The angles between the first and second, second and third, and third and fourth ridges are 40°, 28°, and 55°, respectively. The posterior flange of the pterygoid has a steep medial side and a narrow width. The vomerine tooth is located on a pointed, anteriorly directed base in front of the anterior ridge of the pterygoid tooth plate. No cusps are visible at the margin of the vomerine tooth plate. Only the most posterior end of the parasphenoid is visible between the bones of the shoulder girdle anterior to the ribs.

Opercular and Gular Region.—The counterpart (Fig. 3) shows a large operculum, which is anteroposteriorly longer than dorsoventrally deep (4:3). The suboperculum, preserved on the part below the operculum, is as long as the operculum, but much lower in depth (5:2). The suboperculum is the best preserved bone in the hypotype and has the same shape and size relations as in the holotype.

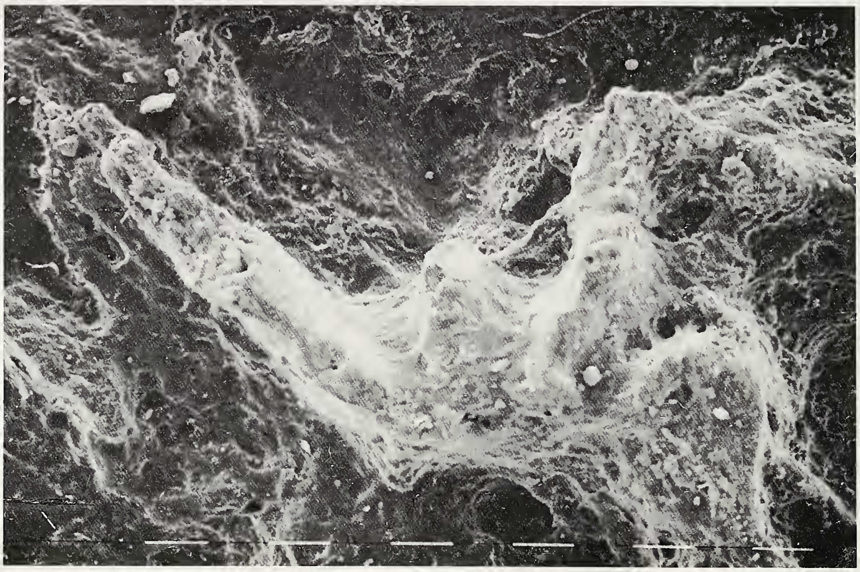

Fig. 4.—*Palaeophichthys parvulus* Eastman, 1908. SEM of Latex cast of holotype MCZ 5090b, left pterygoid tooth plate; ×72 (each white line corresponds to 100 μm).

Part and counterpart show indications of a lateral gular adjacent to clearly preserved principal gulars. The principal gular plate shows striations radiating toward the margin. The ceratohyal is completely visible in the hypotype, but only the posterior part is in the holotype (Fig. 3). It is an elongated bone with narrow middle portion and expanded anterior and posterior ends.

Postcranial Skeleton.—The shoulder girdle of the holotype (Fig. 3) and hypotype consists of a relative short, broad, massive cleithrum and a long, narrow clavicle. The clavicle widens dorsally, where it overlaps the ventral part of the cleithrum. The body of the part and counterpart of holotype and hypotype shows a complete covering of scales. The scales (Fig. 5) are round and elongated, with parallel ridges on the anterior covered field and converging ridges on the posterior exposed field. They show the division in fields typical for post-Devonian dipnoans. Ribs extend posteriorly from the shoulder girdle 40–50% of the body length and indicate the extent of the abdominal cavity. The weakly ossified series of spines extends posteriorly nearly as far back as the ribs.

Paired fins or their traces are not preserved in either specimen. A continuous fin fold surrounds the posterior part of the body. Dorsally it occupies 60% of body length and ventrally 42%. There are no supporting elements visible for the fin fold. The lepidotrichia are not articulated and also seem not to bifurcate.

Age

Lund (1970, 1973) described age pattern in tooth plates of *Palaeophichthys* (*Monongahela*) *stenodonta* and *dunkardensis.* In both species the number of cusps increases with size increase of tooth plates; the cusps are worn in larger tooth plates. The fourth ridge of the pterygoid plate appears late in subadult stage (Lund, 1970:253). This ridge is developed in *P. parvulus,* which indicates that we are dealing at least with subadult, if not adult, specimens, despite their small size.

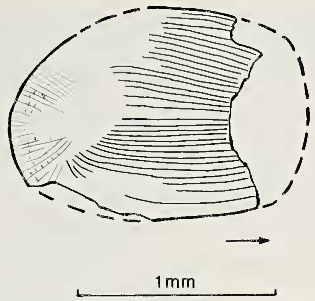

Fig. 5.—*Palaeophichthys parvulus* Eastman, 1908. Scale of holotype MCZ 5090 from the middle of the body above the beginning of the anal fin.

Further indications of subadult or adult stage are the full ossification of skull roof, palate, and ceratohyal; the complete covering of the body by scales; and the lack of cusps on the vomerine tooth.

COMPARISON

Palaeophichthys parvulus is a tooth-plated dipnoan (after the terminology of Campbell and Barwick, 1983), and has no relationship to the denticulated dipnoan *Conchopoma.* The tooth plates of *Palaeophichthys* resemble those of gnathorhizids, and the tooth plate of the pterygoid agrees with the diagnosis of the gnathorhizid genus *Monongahela* (Lund, 1970) in that the most posterior fourth ridge originates laterally to the apex of the tooth plate. On the basis of this evidence, *Monongahela* is, therefore, considered a junior synonym of *Palaeophichthys.* The genus *Monongahela* was described at a time when the true nature and affinities of *Palaeophichthys* were entirely unknown. *Palaeophichthys parvulus* is distinct from the two species *P. stenodonta* and *P. dunkardensis* described by Lund (1970, 1973): it has a different angle between the ridges of the tooth plates, different shape of cusps on the ridges (Table 1), and different position of the fourth ridge. Differences in cusp shape also occur on the vomerine tooth plate. The most posterior fourth ridge of *P. parvulus* originates closer to the apex than in the other two species.

The skull roof pattern of *Palaeophichthys* is unique within Paleozoic dipnoans in having three, possibly four, median unpaired bones (B, C, E, and F): in *Sagenodus* and *Conchopoma* bones B and C are unpaired, but bone E is paired; in *Megapleuron* and *Gnathorhiza* bones B and E are unpaired, but bone C is paired; whereas *Ctenodus* and *Tranodis* have paired C- and E-bones. The composition

Table 1.—*Comparison of the pterygoid tooth plates of the three species of* Palaeophichthys. * *Data from Lund (1970, 1973).*

	Angle between 1. a. 2. ridge (range)	Angle between 2. a. 3. ridge (range)	Shape of cusps on ridges
*P. dunkardensis**	14.37 (7–28)	15.49 (9–32)	rounded
*P. stenodonta**	41.65 (12–60)	48.35	laterally flattened
P. parvulus	40	28	distinct

of the lateral-line bones differs from *Gnathorhiza*: the occurrence of Z-, Y-, X- and elongate KL-bones is more primitive than the reduction to fewer larger bones in *Gnathorhiza* (Berman, 1976). The length/depth relations of operculum and suboperculum also are different in the two genera: the operculum is longer than deep in *Palaeophichthys,* whereas it is deeper than long in *Gnathorhiza.* On the other hand, *Palaeophichthys* possesses a broad cleithrum and a very elongated clavicle, as does *Gnathorhiza* (Berman, 1976).

In summary, *Palaeophichthys* (= *Monongahela*) is distinct in its skull roof pattern from other Paleozoic dipnoans, but the tooth plates indicate close relationship to *Gnathorhiza.*

Conclusions

Palaeophichthys becomes the fourth identifiable dipnoan genus from the Middle Pennsylvanian of the Mazon Creek area, joining *Conchopoma* (Denison, 1969; Schultze, 1975), *Ctenodus* (Baird, 1978), and *Megapleuron* (Schultze, 1977). However, it is now well understood that two ecologically distinct assemblages constitute the Mazon Creek fauna (Johnson and Richardson, 1966). On present evidence, *Palaeophichthys* is restricted to the Braidwood fauna, a nonmarine association that is found in the more northerly area of deposition, including the beds along Mazon Creek in Grundy County. *Conchopoma* and *Megapleuron,* on the other hand, are found only in the marginal-marine Essex fauna, which is best known from Pit Eleven in Will and Kankakee counties, whereas *Ctenodus* is recorded from both assemblages. Although *Megapleuron* is otherwise known only by two specimens from another Pennsylvanian locality in North America (Linton, Ohio: specimen 063.107-2 in David S. Hamilla's private collection) and from the Lower Permian of France, *Conchopoma* and *Palaeophichthys* occur commonly in other Paleozoic localities of North America. *Conchopoma* is known from the Middle Pennsylvanian of Linton (Schultze, 1977; Hook and Baird, 1986) and Five Points (Hook and Baird, in press), Ohio, and from the Upper Pennsylvanian of Vermilion County, Illinois (Schultze, 1977). *Palaeophichthys* was described as *Monongahela* from the Upper Pennsylvanian of Allegheny County and the Lower Permian of Washington County, Pennsylvania (Lund, 1970, 1973). It is surprising that only two specimens of *Palaeophichthys* have been found in the thousands of concretions from the Mazon Creek area.

Acknowledgments

The author is grateful to the chain of persons who delivered the holotype of *Palaeophichthys parvulus* into his hands: Alick D. Walker, Robert W. Hook, Charles R. Schaff, Mary Ann Turner, S. Christopher Bennett, and Donald Baird. Donald Baird contributed to the introduction and prepared the peels. Robert W. Hook, Richard Lund, and Jiri Zidek have helpfully criticized the manuscript. John Chorn kindly photographed the holotype. J. Elder and J. Wiglesworth, Word Processing Center, Division of Biological Sciences, The University of Kansas, kindly typed different versions of the manuscript. The author thanks the National Science Foundation for partial support of the project through grant BSR-8806856.

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